EYE-SPOTS IN DIGENEA.[1]

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INTRODUCTION.

While considerable work has been done on the eye structure of the free-living Plathelminthes and ectoparasitic Trematoda, no adequate study of the eye-spots of the digenetic Trematoda has been made. In fact, although the nervous system of this group has been comparatively well known since the days of Lang (1880), students of Trematoda have been content with the mere mention of the occurrence of eye-spots in this or that species, or at most with a description of an isolated case and perhaps a reference to this organ in Turbellaria or ectoparasitic Trematoda.

There remain unanswered, then, two fundamental questions relative to the eyes of Digenea, (1) What is the fundamental structure of this organ, and (2) how extensive is the development of the organ in the group.

HISTORICAL.

The earliest mention of eye-structure in Digenea was made by O. F. Müller (1773: 68, 70) for *Cercaria lemna*. He suggested that the two black pigment spots of these larvæ were probably eyes. Mehlis (1831) described for the first time pigment eyes in miracidia (*Cathemasia hians*). In 1832 von Nordmann (II., 140) made record of the eye-spots in the miracidia of *Bunodera luciopercæ*. Shortly afterward the X-type of pigment pattern in the embryos of *Fasciola hepatica* and the two beehive spots in the embryos of *Cyclocœlum mutabile* were described. Meanwhile other records of cercariæ with eye-spots had been published. O. F. Müller in 1776 (*C. inquieta*), Hemprich und Ehrenberg in 1831 (*C. alata*), J. Müller in 1850 (*C. setifera* and *C. elegans*), and La Valette St. George in 1855 (*C. ocellata*) for cercariæ, and de Filippi in 1857 for the amphistomulum of

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Diplodiscus subclavatus (Goeze), together with an occasional record of the pigment-spots in miracidia—these observers showed the rather wide distribution of this type of sense organ in the group.

In his second memoir de Filippi (1857: 433) described the pigment spots of *Cercaria echinocerca*. Among the granules, he wrote, were two large pockets of irregular form but symmetrical arrangement on the sides of the esophagus, comparable to the eyes of the amphistome, while within the pigment pocket was a nucleus which represented a veritable rudimentary lens. Leuckart (1863: 465) expressed his credulity about the true lenticular function of the nucleus, but saw the relationship to the eye-spots of ectoparasitic trematodes. He mentioned the occasional presence of such organs in the distome, even in the definitive host. Later (1886: 26) he emphasized their homology to the eyes of the Monogenea.

Accounts of the eye structure in ectoparasitic trematodes have been given by Lang (1880), Goto (1894), Hesse (1897), Beers (1901), and André (1910). Lang worked out the histology of this organ carefully for *Tristomum coccineum*. He found the roots to be a branch of the weak posterior dorsalis, the eye itself to consist of (1) a saucer-shaped pigment cap, (2) a spherical or oval lens, (3) a retinal ganglion cell, and (4) muscle cells. Goto (p. 81) was unable to believe that the eyes of his species were functional because (1) of the position of the pigment granules between the source of light and the lens and (2) because of the degeneracy in part of the lens itself. He was inclined to consider them as temperature sense organs.

In very young cercariæ of *Diplodiscus subclavatus* Looss (1892: 165) found two or three limpid cells with refractive nuclei situated on each side of the esophagus. He thought these to be connected with the developing eye-spots, "die oberste vorzugsweise den lichtbrechenden, die unteren vielleicht die percipirenden Apparate darstellen. Alle drei bleiben aber noch einfache Zellen." Osborn (1903), in connection with the histology of *Cotylaspis insignis*, described eyes for the adults of this species as "located at the front of the pharynx between it and the posterior nerve trunk. . . in close contact with the latter." Each

eye at its best consisted of a pigment cup in which the contents are figured but not recognized as lenticular in function. Monticelli's study (1914) of the eye structure in *Cercaria echinocerca* Fil. is not as clear as the work of the earlier investigator on this species. The eyes in *Cercaria equitator* (Ssinitzin, 1911: Fig. 54) are of interest because they correspond to the X-type originally described for the miracidium of *Fasciola hepatica*. Cort (1915) discussed the eye-spots in monostome and amphistome cercariæ but failed to show their connection with the brain.

Morphology.

The writer has studied intimately the eyes of several monostome and distome cercariæ (Faust, 1917, 1918, 1918*a*). Of twenty-eight species of cercariæ which have come under the writer's observation, seven possess pigmented eyes and four have non-pigmented eyes. The existence of these non-pigmented eyes was first described by the writer for *Cercaria racemosa* and *C. gracillima* (1917).

The eye-spots of the binoculate species are usually in direct connection with the posterior dorsal nerve trunks (Faust, 1918). However, the forked-tailed species, *Cercaria gigas* (Faust, 1918*a*) has connections with the anterior dorsal rami. While the posterior dorsal trunks are, on the whole, much smaller and less important than the corresponding ventral trunks, the ramus to the lateral eye on each side is conspicuous. The cyclopean eye in the trioculate species (confined to certain monostome cercariæ) arises from a fused anterior dorsal nerve trunk. It receives a blunt nerve fiber from below. Thus it differs markedly from the anterior pair of eye-spots in the Monogenea which are innervated by a branch of the same nerve which innervates the posterior pair.

Description of the eye-spot.—In the pigmented eye-spots the pigment consists of a cluster of rather large dark-brown granules, grouped together so as to form a deep cup. At the base of the cup the granules lie several layers deep, but toward the mouth they are seldom more than one layer deep. The opening of the cup in the case of the paired eyes is usually dorsolaterad, whereas the cyclopean eye opens dorsomesad (Fig. 1). Within the pigment

cup is a spherical body, barely touching the pigment granules, opalescent, and containing within it an oval nucleus. This spherical body is the enlarged nerve-cell ending with its nuclues. The nerve may be clearly traced out of the mouth of the pigment cup where it merges into the dorsal branch of the nerve trunk

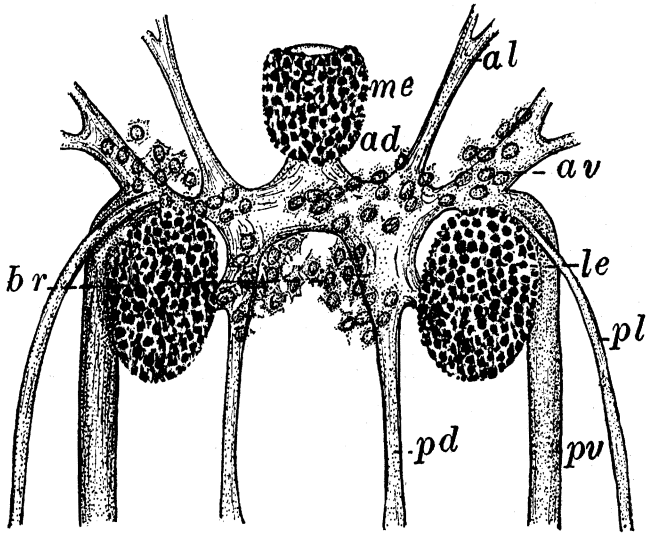

FIG. 1. Dorsal view of the central nervous system of *Cercaria pellucida* Faust, showing paired lateral and cyclopean eye-spots and their connection with the dorsal nerve trunks. *ad*, anterior dorsalis; *al*, anterior lateralis; *av*, anterior ventralis; *br*, ganglion cells; *le*, lateral eye; *me*, cyclopean eye; *pd*, posterior dorsalis; *pl*, posterior lateralis; *pv*, posterior ventralis. × 660.

(Fig. 2). Thus the end organ of this nerve is imbedded in the center of the pigment cup. In the mature cercaria the eye-spot is sunken beneath the basement membrane.

The above description holds likewise for the pigmentless eye-spot, except that in this type of organ no pigment is present. It is recognized in the living cercaria as a round milky body slightly whiter and less transparent than the surrounding parenchyma cells. In stained material its nucleus is conspicuous and its connection with the main nerve center can be made out. In *Cercaria pellucida* although there are ganglion cells scattered superficially along the main nerve trunks no cell is found at the base of the cup. The pigment cup varies in shape from

saucer-shape to deeply pocketed (*C. gigas*). In all cases recorded for the Digenea the opening of the cup is toward the source of light. Thus the organ may function as a light-percipient mechanism, although its function is undoubtedly impaired by the position

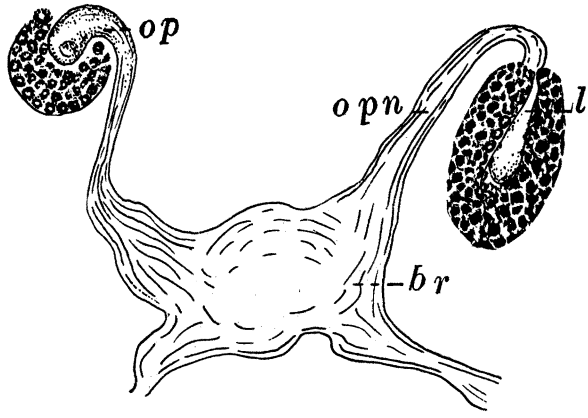

FIG. 2. Section through young *Cercaria pellucida* showing relation of pigment cup to nerve ending in the paired lateral eyes. *br*, brain center; *l*, "lens" of authors; *op*, optic cell; *opn*, optic nerve. × 660.

of the nerve fiber in front of the "lens." This type of eye-spot shows no differentiation into rod and cone structure, such as André (1910) has depicted for *Polystomum integerrimum*. The mechanism at its best is decidedly an inferior one.

DEVELOPMENT.

The pigment eye-spot of the Digenea, as studied by the writer in *Cercaria pellucida* Faust, *C. urbanensis* Cort and *C. gigas* Faust, presents significant points in development. At an early stage of the germ ball it becomes differentiated in accordance with the precocious development of the nervous system in the group. A branch of the posterior dorsalis, with a single nucleus, pushes out from the nerve center to the dorsolateral margin of the embryo. As it reaches a position near the surface somewhat posterior to the cerebral mass, the ectodermal layer of the embryo pushes inward, just posterior to the nerve, so that a pocket is formed with the opening opposed to the nerve cell. The nerve fiber and enlarged end then twist around the inner wall of the

pocket so that the bulbous end with its nucleus comes to lie within the cup (Fig. 3). Although the ectodermal cells of this impocketing are at first visible, they appear to play no further part in the development of the organ. Pigment granules are not present until the nerve ending comes to occupy a position within the pocket. Shortly afterward these granules, at first a golden-brown color, come to be laid down between the nerve ending and the ectodermal cup. As the organ matures the cell with its

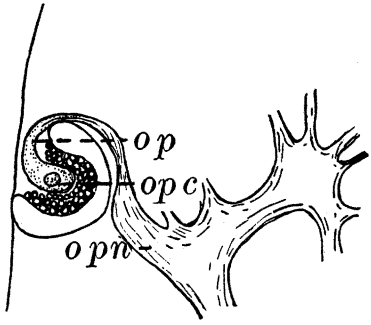

FIG. 3. Section through young germ ball of *Cercaria urbanensis* Cort, showing formation of pigment granules between optic cup and nerve cell. *op*, optic cell; *opc*, optic cell nucleus; *opn*, optic nerve. × 1,460.

nucleus enlarges and assumes the appearance of a lens, although it does not take on concentric rings. The pigment granules become more numerous and darker in color so that *en masse* they look black. Meanwhile the ectodermal pocket becomes less and less conspicuous so that in later embryos it entirely disappears.

While the writer can agree with Looss (1892: 165) that a nucleus is concerned with the formation of the "lens," this nucleus is derived from the nerve center rather than from indifferentiated cells *in situ*. Moreover, the pigment accumulation is not brought about by a secondary nucleus but is the direct result of the apposition of the end organ and the optic cup. Its shape depends on the shape of the optic cup. The melanoidin precipitation is probably a by-product of the nervous system, as has been shown for *Cercaria pellucida*.

The eye-spots are, then, specialized end organs around which a considerable amount of pigment accumulates on account of

increased activity. The pigment is possibly both light- and heat-percipient.

Distribution of Pigment in the Digenea.

For convenience the pigment spots in miracidia, cercariæ, immature and mature trematodes will be discussed separately. Leuckart (1886: 73) states that in general eyes are lacking in miracidia, while Ward (1918) defines a miracidium as possessing an eye-spot. In treating the nervous system of Digenea, Braun (1892) remarks that pigment eyes in adults are exceptional, citing *Acanthopsolus ocellatus* (Levinsen) as the only adult in this order in which eye-spots are known. A survey of the group shows that the data are isolated and in many cases incomplete.

The common examples usually cited in miracidia are the bee-hive pigment eyes of *Cyclocœlum mutabile* and the X-type of *Fasciola hepatica*. Among monostomes it is the common thing to find pigment flecks in the ciliated larva, even in the eggs *in utero*. Among distomes the only species found with pigmented eyes in miracidia are *Fasciola hepatica*, *F. hepatica* var. *ægyptiaca*, *Bunodera luciopercæ*, and *Cathemasia hians* (fide Leuckart). The miracidium of the holostome, *Strigea cornucopiæ* (von Linstow, 1885) possesses conspicuous eye-spots. No record of pigment spots in the miracidia of amphistomes has been found, although Looss (1892, 1896) has worked out the details in the early stages of the life history of four representative species. The miracidia of the Aspidocotylea are not well known.

No pigment eye-spots have been described for the parthenitæ.

Turning to the cercariæ, one is struck by the disproportionally wide distribution of pigmented eyes. In monostomes the cercariæ thus far described possess eye-spots of the binoculate or trioculate types (Fig. 1). Amphistome cercariæ are commonly binoculate. Both monostome and amphistome cercariæ have a considerable amount of pigmentation over the nerve center around the eyes. However, the greatest number of records of eyes in cercariæ concerns the distomes. They are recorded for gymnocephalous species by Ercolani (1881: 54, 55), and Looss (1896: 204–210); for setiferous species by La Valette (1855), Odhner (1914) and de Filippi (1857: 433); for stylet cercariæ by Ssinitzin

(1911) and Faust (1917); for furcocercous forms by La Valette (1855), Sonsino (1897), Cort (1914, 1917), O'Roke (1917) and Faust (1917, 1918*a*); and, in addition, for many other less closely related species by O. F. Müller (1773, 1776), Hemprich und Ehrenberg (1831) and Ssinitzin (1911). Holostome cercariæ have not been shown to possess pigment eye-spots. The existence of the cercaria stage in Aspidocotylea is still uncertain.

After the cercaria stage the pigment may persist for a little while but is usually lost on the arrival of the fluke within the definitive host. However, the pigment granules persist in some cases, being found in the mature worm. Although the pigmentation of the monostome cercaria is carried over to the encysted monostomulum, pigmentation in adult monostomes is quite unknown. On the other hand, several amphistomula which have reached their final host still have a clump of pigment granules around the optic end organ. Among distomes the distomula and adults known to possess pigment eye-spots belong to the Allocreadiidæ or closely related species. In many cases the pigmentation is faint and the "lens" degenerate. No holostome adults are recorded as having pigmented eyes. Whereas the other stages in the life cycle of the Aspidocotylea are in doubt, the group is represented in the adult stage by one pigmented species, *Cotylaspis insignis*.

Reviewing the entire field of the Digenea, pigment eye-spots are found in representative species of all suborders of the Prostomata at one time or another in the life cycle of the individual. Among the monostomes, both miracidia and cercariæ commonly possess these organs. Amphistome miracidia usually lack pigment eyes, while amphistome cercariæ are usually binoculate. Holostome miracidia are pigmented (at least in one species), while neither cercariæ nor adults are pigmented. Few distome miracidia are marked by pigment eye-spots, although a pigmented optic organ is common in cercariæ of various distome families and usually present in Allocreadiide distomula and adults. The only recorded instance of pigmented eye-spots in miracidia, cercariæ, and adults is that of *Bunodera luciopercæ*.

TABLE SHOWING PIGMENTED EYE-SPOTS IN DIGENEA.

Group.	Miracidium.	Cercaria.	Adult.
Gasterostomata.....	none	none	none
Prostomata			
Aspidocotylea.....	?	?	present in *Cotylaspis insignis*
Monostomata.....	common	common	none
Amphistomata....	none (?)	common	in amphistomula and some adults
Distomata.....	seldom	common	in Allocreadiide species
Holostomata.....	in *Strigea cornucopiae*	none (?)	none (?)

GENERAL CONSIDERATIONS.

The occurrence of eye-spots in various stages of the life cycle of Digenea and in representative species of all suborders of the Prostomata at one time or another in the life cycle show the fundamental significance of the eye structure. The preservation of the pigmentation and of the "lens" in this or that group has been decidedly erratic and apparently unrelated to the systematology of the group. The great trend has been one of degeneration. If the sporocyst or redia ever possessed eye-spots they have lost all vestiges of them. The absence of eye-spots in many cercaria-trematode generations shuts out any clue of pigmentation at a former period. In some cases absolutely no evidence exists in the life cycle of a possible former pigmentation. In spite of these facts, the widespread pigmentation throughout the Digenea warrants the belief that pigmentation was general throughout the Class at some former time.

In most cases pigment eye-spots have been described because they were conspicuous. It is highly probable that in many species pigmentless eye-spots exist. The three cases on record (*Cercaria racemosa*, *C. gracillima* and *C. minor*) were found only by a most careful study of the worms under high powers of the microscope. While they are undoubtedly functionless, a record of their existence extends the knowledge of the extent of eye-spots and of the types of degeneration that have occurred under conditions of endoparasitism.

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